

# Objective classification of latent behavioral states in bio-logging data using multivariate-normal hidden Markov models

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**Abstract.** Analysis of complex time-series data from ecological system study requires quantitative tools for objective description and classification. These tools must take into account largely ignored problems of bias in manual classification, autocorrelation, and noise. Here we describe a method using existing estimation techniques for multivariate-normal hidden Markov models (HMMs) to develop such a classification. We use high-resolution behavioral data from bio-loggers attached to free-roaming pelagic tuna as an example. Observed patterns are assumed to be generated by an unseen Markov process that switches between several multivariate-normal distributions.

Our approach is assessed in two parts. The first uses simulation experiments, from which the ability of the HMM to estimate known parameter values is examined using artificial time series of data consistent with hypotheses about pelagic predator foraging ecology. The second is the application to time series of continuous vertical movement data from yellowfin and bigeye tuna taken from tuna tagging experiments. These data were compressed into summary metrics capturing the variation of patterns in diving behavior and formed into a multivariate time series used to estimate a HMM. Each observation was associated with covariate information incorporating the effect of day and night on behavioral switching.

Known parameter values were well recovered by the HMMs in our simulation experiments, resulting in mean correct classification rates of 90–97%, although some variance–covariance parameters were estimated less accurately. HMMs with two distinct behavioral states were selected for every time series of real tuna data, predicting a shallow warm state, which was similar across all individuals, and a deep colder state, which was more variable. Marked diurnal behavioral switching was predicted, consistent with many previous empirical studies on tuna.

HMMs provide easily interpretable models for the objective classification of many different types of noisy autocorrelated data, as typically found across a range of ecological systems. Summarizing time-series data into a multivariate assemblage of dimensions relevant to the desired classification provides a means to examine these data in an appropriate behavioral space. We discuss how outputs of these models can be applied to bio-logging and other imperfect behavioral data, providing easily interpretable models for hypothesis testing.

**Key words:** autocorrelation; behavioral ecology; bio-logging; diving behavior; fisheries; hidden Markov models; state-space models; tagging; time series; tuna.

## INTRODUCTION

The study of ecological systems often necessitates the analysis of complex data, in which processes are not explicitly observed despite the emergence of signals and patterns. Such data can indicate the approach of ecological tipping points (Lenton 2011), future ecosystem states (Luo et al. 2011), or the ecology of individual organisms (Block et al. 2011). In order for this information to be incorporated into natural resource management models and strategies,

quantitative tools for the objective description and classification of time series from ecological systems are needed (Morales and Ellner 2002, Harwood and Stokes 2003).

An example of such data is found in the behavioral study of wild free-ranging animals, which has been revolutionized over the last two decades by the development of bio-logging equipment. High-resolution records of the temporal and spatial behavior of animals are now available in unprecedented quantities (e.g., Hammerschlag et al. 2011), allowing the potential for numerical relationships between species behavior and the environment to be quantified (e.g., Mori and Boyd 2004, Block 2005, Choquenot and Forsyth 2013, Evans et al. 2013). The information captured from bio-logging

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experiments is now used in ecosystem and population dynamics models for those species providing important economic or cultural ecosystem services (Lehodey et al. 2008, Maury 2010, McLane et al. 2011). However, three problems typically arise when carrying out analyses of these data.

First, although bio-loggers can record high-resolution data relating to individual movement, the behavior of the tagged animal is not explicitly observed. Changes in movement patterns are the likely result of underlying motivational changes in animal behavior. These motivations may persist or change in relation to environmental or other stimuli, but because these interactions are not directly observed, considerable care must be taken when interpreting time-series data recovered from bio-logging deployments.

Second, behavioral time-series data contain significant autocorrelation; i.e., behavior observed at one time is related to behavior observed previously. This is a result of the persistence of the underlying processes, such as hunger or resting, that motivate the animal's behavior. The presence of autocorrelation means that traditional statistical tools, based on the assumption of independent observations, may be unreliable (Hartmann and Gottman 1980, Jassby and Powell 1990).

Finally, characterizing behavioral states from time-series data requires the analyst to classify and describe distinct patterns, and to identify or smooth noise in the data (Hartmann and Gottman 1980). When undertaken manually, each of these stages can introduce conscious and unconscious biases to the interpretation of this behavior. Arriving at an objective description, however, is problematic, and care must be taken when choosing the correct temporal and spatial scale to examine inferred behavioral patterns in light of the specific hypotheses being tested (Levin 1992).

Free-roaming marine species present a particular challenge in this case. Detailed information on the movements of these animals can be captured with bio-logging equipment (see Plate 1), but much of the environmental and ecological context of the behavior is hidden from us (Kirby 2001). Their movements may be relatively unconstrained both laterally and vertically, their spatial ranges are often large, and behavioral cues are less familiar (Dagorn et al. 2001, Davies et al. 2012). Dynamic environmental boundaries such as ocean fronts constrain or promote spatial behavioral patterns that are often transient and relatively unpredictable (e.g., Gaspar et al. 2006, Bost et al. 2009, Tew Kai et al. 2009). This poverty of information makes the already imperfect signals observed from bio-logging experiments on these animals especially difficult to interpret.

Continuous dive data can be considered as measurements of depth and temperature captured at the scale of minutes in a single vertical dimension, and which exhibit no consistent behavioral unit of division. In fish species,

for example, these vertical movement data are not structured according to any convenient unit of behavior such as surfacing to breathe, marked individual dives, or returns to a nest or colony. Such data captured from bio-logged apex predators contain patterns of diving that are hypothesized to be driven by foraging, predator avoidance, and physiological regulation (Schaefer et al. 2007, Campana et al. 2011, Hazen et al. 2011). However, because it is nearly impossible to measure environmental context and stimulus at depth for free-roaming animals, there is at present no consistent method of describing these kinds of data.

Hidden Markov models (HMMs) are a form of state-space model that have been increasingly applied to time series of animal movement that are hypothesized to indicate distinct behaviors. Hidden Markov modeling has had a long history in the field of signal processing, particularly for voice recognition (Gales and Young 2007), but its popularity as a tool for examining ecological data has increased in recent years. Examples of such models applied to ecological problems include the foraging behavior of mouse lemurs (Schliehe-Diecks et al. 2012), the spawning success of shovelnose sturgeon (Holan et al. 2009), at-sea behavior of Manx Shearwater (Dean et al. 2012), and diving behavior in Macaroni Penguins (Hart et al. 2010). HMMs assume that observations will depend on a finite number of underlying unobservable states (MacDonald and Zucchini 2009). Accordingly, each individual observation is assumed to be drawn from one of several distributions, each corresponding to a "hidden" state. In the case of animal behavior, one might assume that an individual has resting and feeding states, each associated with distinct distributions in the data recorded by a bio-logging device. The underlying principle is analogous to an independent or discrete mixture model (Welsh et al. 1996), in which observations are drawn from one of several independent distributions in proportion to a probability for each state. In a HMM, however, the transition between hidden states is assumed to be governed by a Markov chain, where the probability of the animal being in a given state at a given time is dependent on the state it was in during the previous time step. Autocorrelation is therefore intrinsically incorporated into the assumptions of the model, albeit with an assumption of first-order Markov dependence.

Here, a further extension of these methods is described for processing, describing, and classifying time series using first-order multivariate normal HMMs for the analysis of continuous dive data from bio-logging devices. The HMMs applied in this study model three aspects of the patterns found in the data. First, the most likely parameters describing the state distributions are estimated, indicating the shape of the observation model associated with each state. Second, the parameters that describe the probabilities of switching between these underlying states at any time step are estimated.

Third, the fully described HMM can then be used to probabilistically classify the time series into a state at each time step.

In contrast to building biological models that explore physiological drivers of behavior (e.g., Malte et al. 2007), our aim was to apply a classifier that can quantitatively describe and identify the different kinds of behavioral patterns that are observed in continuous dive data. We arranged multidimensional bio-logging data sets into a number of discrete, state-dependent and multivariate observation models, linked to a state-switching mechanism. We examined the effect of covariate information by incorporating it directly into the parameters of the matrix of state-switching transition probabilities. This approach is similar to that described in Holan et al. (2009), where a hierarchical Markov switching model was fitted to behavioral data captured using bio-logging devices to predict spawning of shovelnose sturgeon using covariate biological data. Our study was motivated by a need to more objectively quantify the behavior of tropical tuna, in the context of providing scientific advice for the management of an important natural resource, namely tuna fisheries in the Western and Central Pacific Ocean. Initially we describe and explore our method by simulating data that represent two potential scenarios for the ecology of a theoretical marine animal. HMMs were fitted to these artificial data, and their performance was examined. We then applied the same approach on a small sample of data sets recovered from archival tags implanted in two species of commercially important tropical tuna, and compared the estimated behavioral states and state-switching with previous descriptions of these species' behavior.

MATERIALS AND METHODS

Detailed mathematical descriptions of HMMs and broader state-space models exist in previous publications (e.g., MacDonald and Zucchini 2009, Patterson et al. 2009), but the basic concepts are outlined here. In the context of animal behavior, a HMM assumes that an observation,  $X$ , at a particular time step (e.g., distance traveled, speed, or location) is drawn from a distribution,  $\mathbf{D}$ , associated with a behavioral or motivational state  $S$ . In addition, the time series of these behavioral states forms a Markov chain that is described by a matrix of probabilities governing the switching between states. The probability of an individual occupying a behavioral state at time  $t$  is dependent on the probabilities of occupying each of the states at time  $t - 1$ . Although we do not explore them here, more complex  $q$ -order dependence can also be incorporated in a variety of ways, by including the mixture transition distribution models proposed by Raftery (1985), or expansion of the transition matrix to allow each state to be defined as a vector containing the states of the previous  $q$  time steps.

In a HMM, the state at each time step  $S_t$  will be one of  $M$  states  $i$ , each associated with a separate probability distribution  $\mathbf{D}$  with parameters  $\phi_i$ . The probability (Pr) of observing  $x_t$  is therefore:

$$\Pr(x_t | S_t = i) = \mathbf{D}(x_t | \phi_i). \tag{1}$$

The hidden process model in a HMM that controls the switching between these states from time  $t - 1$  to time  $t$  is described by a set of state-to-state transition probabilities grouped in a transition matrix  $\mathbf{\Gamma}$ , which simply arranges the probabilities of switching from the current state to each of the others at each time step. Each transition from state  $i$  to state  $j$  is a transition probability,  $\pi_{ij}$ , collected together in the transition matrix which describes the probability of switching from any state to any other:

$$\mathbf{\Gamma} = \begin{bmatrix} \pi_{11} & \dots & \pi_{1M} \\ \vdots & \ddots & \vdots \\ \pi_{M1} & \dots & \pi_{MM} \end{bmatrix} = \Pr(S_t = j | S_{t-1} = i). \tag{2}$$

Following the law of total probability, each row of this transition matrix describes all possible switching outcomes from a given state, that is,  $\pi_{ij}$  must sum to 1 across  $j$ .

In general, the likelihood of a given set of time-series data from  $t = 1 \dots T$  is the joint probability of observing the observation sequence

$$L_T = \Pr(x_1, x_2, x_3 \dots x_T). \tag{3}$$

Although the joint probability is the product of each individual observation probability, the sum of the logarithms is usually taken. In a HMM, this joint probability can be decomposed as follows. The state probability,  $\Pr(S_t)$ , is dependent on the state probabilities at  $t - 1$ . Consider the likelihood contribution at time  $t$ :

$$\begin{aligned} L_t &= \sum_{i=1}^M \left( \Pr(x_t | S_t = i) \Pr(S_t = i) \right) \\ &= \sum_{i=1}^M \left( \Pr(x_t | S_t = i) \Pr(S_t = i | S_{t-1}, x_{t-1}) \right) \\ &= \sum_{i=1}^M \left( \Pr(x_t | S_t = i) \Pr(S_t = i | S_{t-1}) \Pr(S_{t-1} | x_{t-1}) \right). \end{aligned} \tag{4}$$

The likelihood contribution of each observation is therefore the sum of probabilities of observing this observation for each behavioral state distribution, given the probability that the individual is occupying that state, dependent on the state occupied at the previous time step. During parameter estimation, the negative log-likelihood was minimized using a multi-

variate adaptation of the forward-filtering recursive algorithm described in Patterson et al. (2009) and MacDonald and Zucchini (2009). The classification probability of each behavioral state at each time step is undertaken using the state probability backward-smoothing approach detailed in Wikle and Berliner (2007).

#### *Covariate information*

It is also possible to include further covariate information in the estimation of these model parameters. A covariate that is assumed to affect the value of a parameter can be included as a coefficient in an equation describing how that parameter changes in relation to the covariate. Here only binary information is included to assume a linear relationship between the covariate and the state-switching probabilities. In this case, for each individual transition probability defined in Eq. 2:

$$\pi_{ij} = \alpha_{ij} + \beta_{ij}\gamma \quad (5)$$

where  $\gamma$  is a continuous or binary covariate, and both  $\alpha$  and  $\beta$  are estimated parameters. In the case of the binary covariates we use here, the result is that each state transition probability assumes one of two different values, depending on the value of the covariate. It is also possible to include similar covariate parameters in the state distribution mean parameters, allowing the nature of the states themselves to change in relation to covariate information. However, for simplicity of our example application here, we assume constant state distribution parameters across the time series.

For fitting HMMS to behavioral time series captured from bio-logging devices that record data on water depth and temperature, we use a mixture of multivariate normal distributions to model the multi-dimensional data sets. Thus this observation model replaces the generic distribution in Eq. 1, and is a state-dependent multivariate normal distribution of  $k$  dimensions, such that we assume for each observation  $x_t$

$$x_t \sim \mathbf{D}(\varphi_i) = \mathbf{N}(\mu_i, \Sigma_i) \quad (6)$$

where  $i$  is the current hidden state,  $\mu_i$  is the multivariate mean in  $k$  dimensions, and  $\Sigma_i$  is the  $k$  by  $k$  variance-covariance matrix.

#### *Data pre-processing*

For the HMMS in this study, data were assembled into a two-dimensional space where each axis represented a summary metric calculated from dive profiles that had been separated into temporal bins. Our method involved three stages of data pre-processing. First, raw dive data were divided and compressed to a time series of these summary metrics. Temporal binning and metrics were chosen to capture the variation of patterns in the dive profile, representing relevant dynamics and

temporal scale to the behaviors we wished to examine. These summary metrics were then log-transformed to approximate a mixed-normal distribution, and finally arranged as a multivariate time series.

It is important to match the temporal scale of observations to the temporal scale of the behaviors that are the focus of the investigation and the specific questions being asked. Working with raw dive data provides many observations, but exhibits high levels of variation and short-term behaviors, such as thermoregulatory ascents (Holland et al. 1992). Although an examination of these short-term activities using HMMS based on raw high-resolution dive data may certainly be valuable, here we investigate behavior that occurs within a time frame of approximately three hours. We assume that this is the temporal scale that concerns feeding, digestion, and satiation (Olson and Boggs 1986), as well as fishing events (Baird 2009). The choice of timescale has the potential to add uncertainties that are not accounted for within the HMM method. Exploratory analyses that vary the temporal intervals used for summary metric calculation are advisable to ascertain the possible influences on results in a full analysis. For our study, alternative HMMS were also estimated on the same time series processed into 1-h and 12-h subsections. Although statistically significant differences were seen in these alternative multivariate-state distribution and transition parameter values compared to 3-h sectioning, the appropriate number of states and general description of estimated behaviors remained the same. At 1-h sectioning, multivariate distributions had smaller variance-covariance matrices and slightly less consistent transition matrices across individuals. At 12-h sectioning, multivariate distributions were larger due to more variable patterns within each bin, but had transition matrices very similar to those of the 3-h sectioned HMMS. Our aim was to present a description of behavior at a scale that was relevant to fishing events, i.e., at the scale of 1–5 h, and that could be compared with descriptions of tropical tuna behavior from previous studies. In the current study, the raw depth and temperature continuous time-series data were therefore divided into 3-h subsections.

This temporal sectioning was undertaken by first making divisions each day at dawn and dusk, estimated using a split-moving-window analysis (Ludwig and Cornelius 1987) on proportion of time at depth. This approach, which estimates points of significant change in a one-dimensional signal, has been used elsewhere to divide the vertical behavior of animals into sections over longer timescales (Humphries et al. 2010). Three further divisions were made between the initial boundaries estimated for dawn and dusk, creating eight subsections of approximately three hours across a 24-h period. Sensitivity of this 3-h interval was also examined by summarizing the data across a range of time bins, with no discernable improvement for higher

resolutions in the interpretation of the time series for the purposes of our example application (see Appendix A).

Summary metrics were calculated from each 3-h subsection to form the observations from which the HMM was estimated. Any number of summary metrics can be chosen to form the multivariate arrangement of observations, but in this study a two-dimensional observation model was chosen. Median temperature was selected as a measure of habitat that was an alternative to absolute depth, and the standard deviation of depth experienced (a proxy for amplitude in the dive profile) was chosen to quantify variation in movement through the water column.

The summary metrics from each time series were log-transformed to better approximate a mixture of normal distributions. These processed data were then arranged as a two-dimensional multivariate assemblage, forming the time series of observations to be modeled by the HMM. Although covarying, the multivariate observations we have chosen represent both a thermal habitat in the water column and the strength of association at that depth. In addition, each observation was associated with a binary covariate indicating the diel state, either day or night, at the time of observation. This binary information was used as a coefficient in the estimation of all transition matrix parameters, resulting in HMMs that essentially contained two sets of transition probabilities between states, one each for day and night. A complete description of this data pre-processing is given in Appendix A.

#### *Model estimation and selection*

For each data set, a series of HMMs with two to five assumed hidden states was estimated. In addition, a single-state model was estimated consisting of a lone multivariate normal distribution without the transition matrix Markov chain component. Model parameters were estimated using the numerical estimation of a minimum negative log-likelihood described in Patterson et al. (2009), and using the Nelder-Mead algorithm in the R (R Core Team 2013) function *optim()* (Nelder and Mead 1965), set to a tolerance  $1 \times 10^{-4}$ . The results of the simulation experiments suggested that *optim()* was a suitable parameter optimization technique for our tropical tuna example, but if similar experiments fail to accurately converge for other applications, then more complex nonlinear optimizers should be considered. Initial values were supplied by using a *k*-means algorithm (MacQueen 1967, Hartigan and Wong 1979) to cluster the multivariate assemblage into the same number of groups as states assumed in the model. Starting values for multivariate means and variance-covariance parameters were calculated from these clusters, and a transition matrix was created from the observed sequence of these classified observations. Modeled transition parameters were transformed using

an additive logit function, constraining each  $\pi_{ij}$  to between 0 and 1, and summing to 1 across each *j* assumed in the model. State distribution parameters were estimated, and are shown, in log-space, although when we refer to the specific distribution means, these values are back-transformed.

A number of techniques can be used to select the most appropriate model from this suite for a given time series. Using Akaike information criteria on independent mixture models has been found to result in overestimation of the number of states and to be an unreliable indicator of model suitability (Celeux and Soromenho 1996, McLachlan and Peel 2004). To avoid similar potential problems selecting the most informative HMM from a suite, we instead identified marked rates of increase in the estimated likelihood across increasingly complex models. As the number of predetermined hidden states increases, the estimated likelihood value tends to also increase due to the higher number of model parameters fitting to the data more tightly. However, a distinct “knee-bend” can be seen in measures of the likelihood across these models as increased numbers of parameters result in smaller improvements in the model fit (Zhao, Xu and Franti 2008, Dean et al. 2013). Likelihood estimates from models with a greater number of states than occur at this “knee-bend” are likely to be over-fitted.

In addition we used a visual inspection of “pseudo-residuals.” MacDonald and Zucchini (2009) introduce these quantities, aiming to fulfil a model-checking role similar to that of the residuals in conventional statistical models. In a HMM, we do not aim to predict the value of a response variable, but rather the nature and probability of observations being a result of the assumed underlying states. As such, there are no residuals in the sense of the difference between predicted and observed values. However, the distribution of pseudo-residuals can be used to examine the appropriateness of a model. They can be defined as the probability, assuming the state distributions and probabilities of the estimated model, of obtaining an observation less than or equal to each individual observation, and should be uniformly distributed for appropriate models. A more complete description of pseudo-residuals is given in MacDonald and Zucchini (2009).

#### *Simulation experiments*

Validating the effectiveness of HMMs for identifying true behavioral states from associated indirect measurements is challenging, because it requires a priori knowledge of the true behavioral states associated with the time-series data. In the absence of suitable data from animal studies, virtual “simulation experiments” were conducted to develop and examine the effectiveness of using HMMs to estimate parameters that can be compared with true known values. Following this, our method was applied to a small

sample of real bio-logging data taken from two species of tropical tuna.

Consider a theoretical free-roaming animal, capable of spending extended periods of time at depth in cold oxygen-depleted layers of water. The feeding ecology of this individual is based on active predation on vertically migrating prey, which spend the nighttime located in a relatively narrow mixed surface layer, but which are patchily distributed throughout the water column during the day. When a patch of prey is found, the individual will associate with the patch for a period of time, feeding until either it is satiated or the patch disperses, across a temporal scale of hours. Our simplified system is constructed to be analogous to the general behavior of many large marine predators in oligotrophic waters (Dagorn 2000).

It is assumed that our individual has been tagged with a bio-logging device capable of recording high-resolution data for depth variation and water temperature at the scale of minutes, and that we process this information to give us summary values for these data at 3-h intervals. We simulate two scenarios and estimate HMMS, using replications of each to examine the effectiveness of recovering true parameters.

In the first scenario, our individual alternates between two behavioral states: feeding on prey in a narrow band of warm shallow water, and feeding on prey across a variety of deep cooler water layers. These behaviors are somewhat persistent, as the individual finds patches of prey and associates with them to feed. A conceptual diagram of these behaviors and summary observations is shown in Fig. 1.

In the second scenario, our individual follows similar behavior, except that it is now capable of enduring significant time at depth, feeding on patches of prey in very deep cold water. There are now three behavioral states: two persistent feeding states and a third transitive state, representing movement throughout the water column while searching for patches of prey. Furthermore, switching between these states is linked to a cyclic binary covariate representing a daytime and nighttime cycle. Feeding in the shallows is more persistent during the night, while feeding at depth is more persistent during the day.

We stochastically generated 50 time series of observations from multivariate normal distributions and transition matrices to create time series representing the processed data from each of these two scenarios. Each time series was of length  $N = 500$  observations, which is analogous to over 60 days of data from a bio-logging device, assuming our resolution of mean values calculated at 3-h intervals. The true multivariate normal distributions, alongside mean estimates from the HMM, are shown in Fig. 2. A detailed list of the parameters is given in Appendix B.

#### *Real-world data*

Having examined the success of using multivariate HMMS on simulated time series, we then applied this

method to real-world data. Time series were chosen from six individuals across two species of tropical tuna: three *Thunnus albacares* (yellowfin tuna, see Plate 1), and three *T. obesus* (bigeye tuna) tagged and released in the Western and Central Pacific Ocean on separate occasions spanning February 2007 to December 2011. The vertical behavior of these species has been described in numerous previous studies (e.g., Ohta and Kakuma 2004, Dagorn et al. 2006, Schaefer et al. 2007), exhibiting some differences in their evolved strategies to exploit prey through the water column (Dagorn 2000). We have chosen these species in part because of the need to incorporate quantitative measures of their behavior in models for natural resource management, but also because across species and size classes, they exhibit behaviors that can be difficult to distinguish, some being constant and others variable (Schaefer et al. 2009, Robert et al. 2012, Matsumoto et al. 2013).

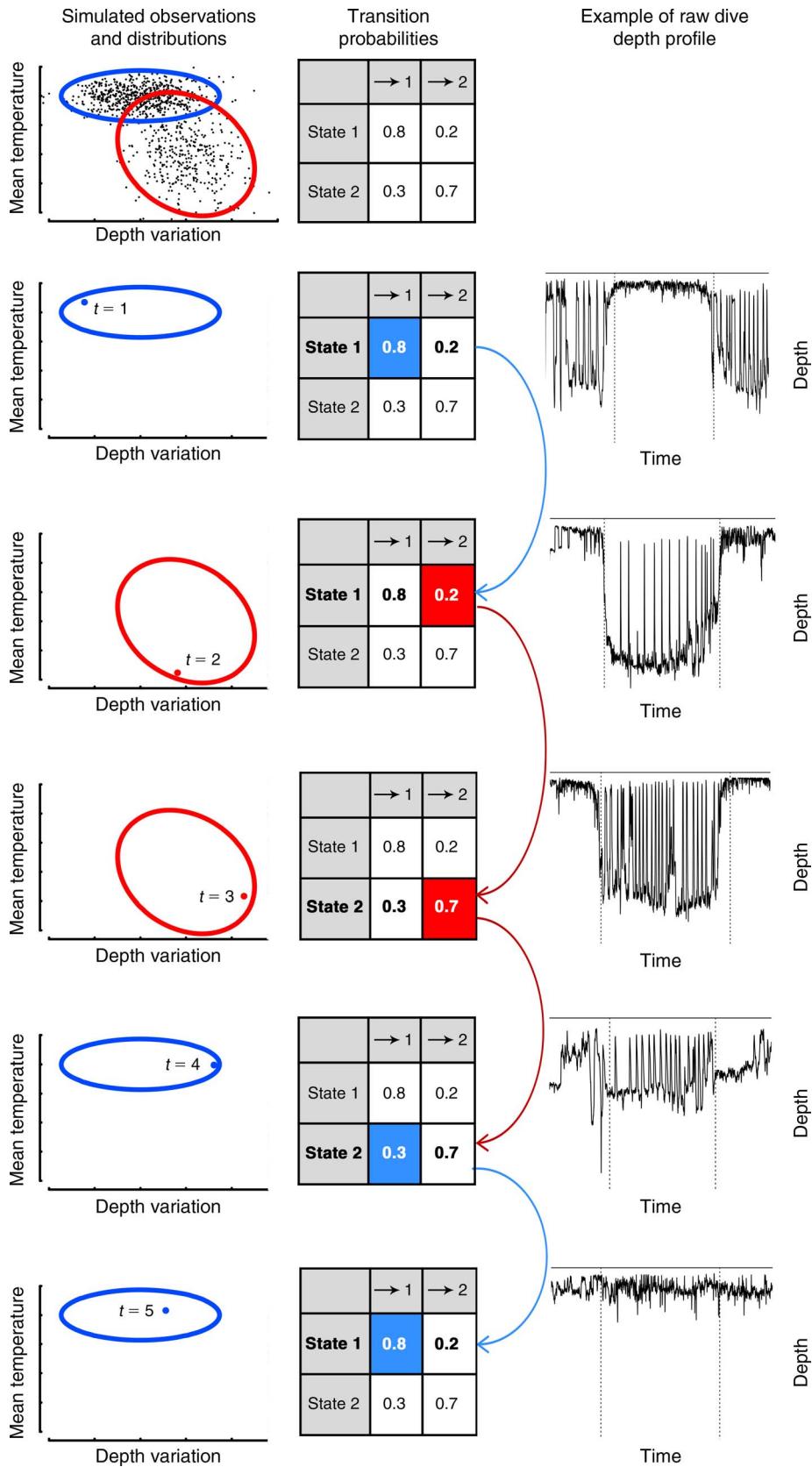
A data set of bio-logging data from these species has been collected by the Pacific Tuna Tagging Programme (PTTP). The behavioral time series used in this study are taken from this database, and were recorded by archival tags surgically implanted in tropical tuna following the methods outlined in Schaefer et al. (2007). A variety of electronic tag devices were used, and each time series is summarized in Table 1.

## RESULTS

### *Simulation results*

We examined the results from the two simulation experiments before building HMMS on the time-series data from real bio-loggers. The average negative log-likelihood values from the 50 repetitions across HMMS estimated with a successively greater number of hidden states are shown in Fig. 3. A visual inspection of these values, alongside pseudo-residuals, showed little improvement for models in which the number of assumed states was greater than the true number used in the two scenarios. These true values were two and three states for scenarios one and two, respectively.

The true and average estimated state distributions across the 50 replications of these “correct” models for each simulation scenario are also shown in Fig. 2 (summary statistics are given in Appendix B). Quantifying the performance of the HMM estimation is nontrivial. Although many common statistical tests exist for comparing sample means to a population mean, for multivariate distributions more complex measures such as Kullback-Leibler divergence must be used (Kullback and Leibler 1951). In these simulation experiments, however, we simply wish to examine the accuracy of our method for recovering the known parameter values used in the simulation of our data. Here we use parallel coordinate plots (Inselberg 1985) to visually examine the accuracy and variation of the estimated models in these simulation experiments. These plots are used for



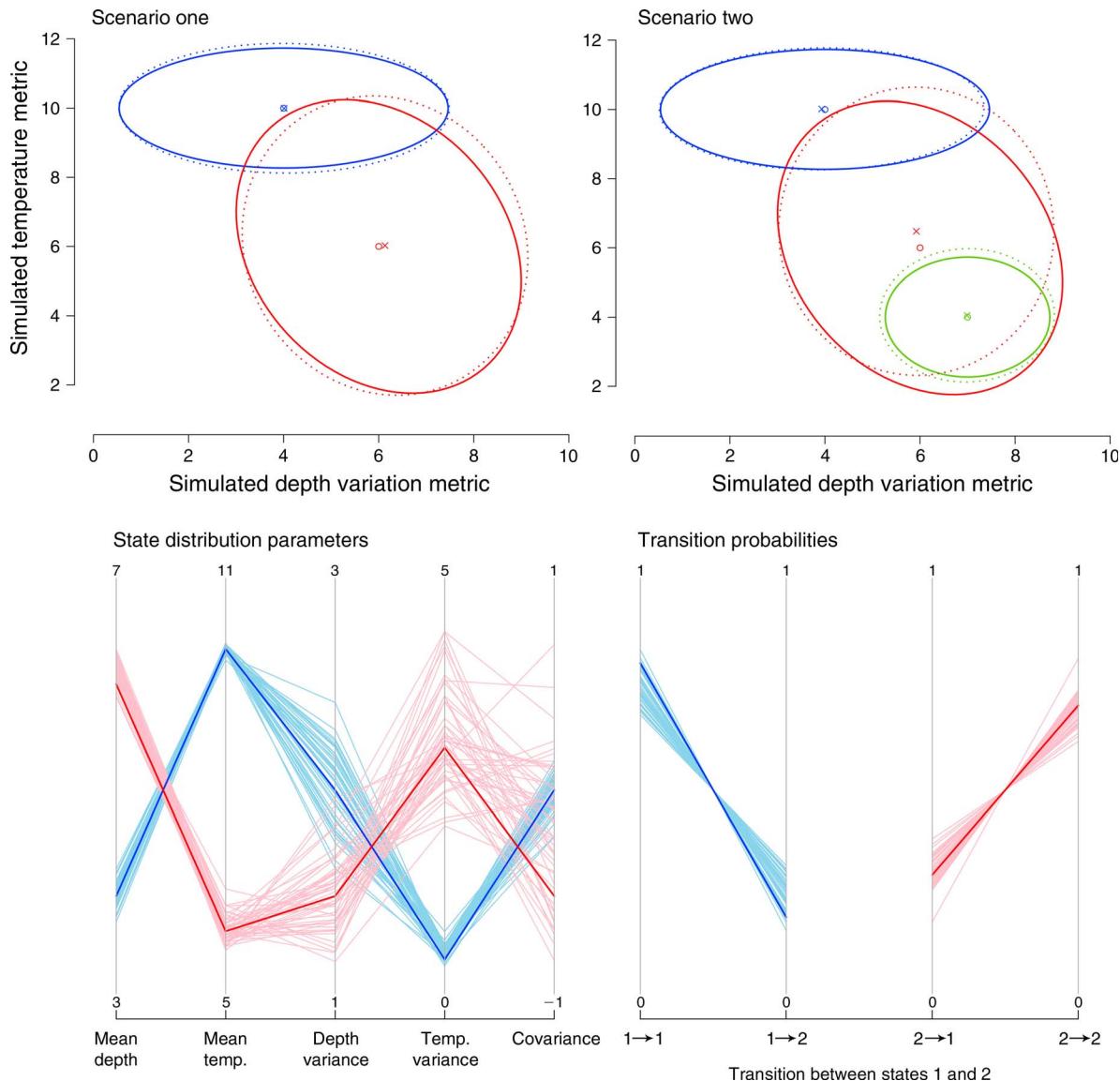


FIG. 2. Results from the simulation experiments. True parameters for each state are shown with solid lines of one color, and model estimations with faint dotted lines of the same color; Symbols indicate the mean true values (open circles) and mean estimated values (×) for each state. The top row shows the true and mean estimates of the state distributions in their multivariate space. Scenario one is described in Fig. 1. Scenario two is described in *Materials and methods: Simulation experiments*. The bottom row shows parallel coordinate plots for the true and estimated values of each parameter in scenario one (scenario two is given in Appendix A). Each column represents a different parameter in the model. States are colored differently, with true values shown by solid lines and the estimated values for each replication shown by faint lines. For all panels, parameter values are arbitrary and unitless, for simulation purposes.

FIG. 1. Conceptual diagram of a single repetition of simulation scenario one for the first five time steps ( $t$ ), in which the individual (a theoretical marine animal) alternates between two behavioral states (blue and red). The top left panel displays all of the simulated multivariate observations, along with the two true state distributions; lower panels in the first column display observations and true state distributions over the five time steps. The second column is the true matrix of transition probabilities, with arrows showing the simulated state-switching between time steps. The boldface type shows the current state of the system. The third column gives potential patterns these observations could represent in real dive tracks (data from tropical tuna dive profiles); scale numbers are not shown.

TABLE 1. Summary of time series from bio-logged tropical tuna used in the example application.

Fish	Species	Release fork length (cm)	Available days of data	Recording resolution (s)	Date of release	Notes
Arc163	bigeye	59	174	240	Nov 2011	Lotek Wireless LTD-2510
Arc294	bigeye	53	318	30	Dec 2011	Lotek Wireless LAT-2810
Arc272	bigeye	106	360	30	Nov 2010	Wildlife Computers TDR-Mk9
Arc88	yellowfin	50	168	300	Feb 2007	Lotek Wireless LTD-2410; initial 40 days of data corrupt and removed
Arc269	yellowfin	98	255	30	Jun 2010	Wildlife Computers TDR-Mk9; ~240 days data corrupt and removed
Arc220	yellowfin	98	124	60	Sep 2007	Wildlife Computers TDR-Mk9

Notes: Fork length is the straight-line measurement from the tip of the snout to the edge of the central caudal fin rays. The TDR-Mk9 tags are from Wildlife Computers, Redmond, Washington, USA; the Lotek tags are from Lotek, Newmarket, Ontario, Canada.

displaying multidimensional data, with the position of each point marked by a line that passes through each vertical bar at the position of that point in each dimension. The true and estimated values of each set of state distribution parameters alongside transition probabilities for scenario one are shown in Fig. 2 (see Appendix B for the corresponding figure for scenario two).

In general the state distribution parameters were well estimated by the models, with multivariate means estimated more accurately than variance-covariance matrices. Less persistent states, having generally fewer observations, had less accurately estimated parameters. Large, dimension-specific variances were not precisely estimated, although they were normally distributed around the true values. In addition, although covariance values of zero were well recovered, when levels of covariance between dimensions were nonzero, these values were both less precisely and less accurately estimated. Transition parameters were also well estimated, although states with few observations or high overlap with other distributions were naturally less precise. In the case of scenario one, the estimated HMMs had a mean correct classification rate of 97.0% (SD 0.9%), and for the more complex scenario two, the mean was 90.6% (SD 3.4%).

*Real-world data*

The same model selection criteria of identifying reduced decrease in negative log-likelihood across models with an increasing number of states (Fig. 3), as well as an examination of the pseudo-residuals, was carried out on models of the wild tuna. In all cases, the most appropriate HMM was one that assumed two behavioral states. These states can be considered as either warm or cold, dependent on the value of the state distribution mean in the median temperature dimension. Fig. 4 shows the estimated state distributions for all individuals, divided into these warmer and colder categories.

The estimated warm states were very similar for all individuals, exhibiting a spectrum of depth variation but occupying a similar temperature range. The cold states were more different across individuals, with distribu-

tions clearly centered in colder water for the bigeye tuna compared to the yellowfin. In contrast, depth variations were less variable across cold states, and all distributions were centered at a greater standard deviation of depth than in the warm states.

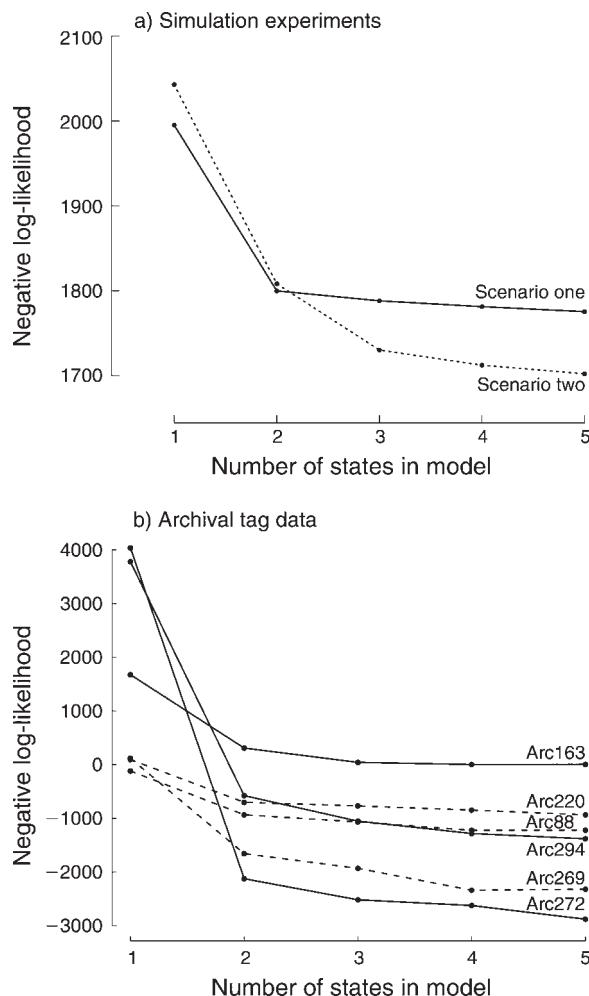


FIG. 3. Reduction in negative log-likelihood scores across models with increasing numbers of states. Results are shown (a) from the simulation experiments and (b) from all archival tag time series examined in this study, where individual tuna are identified by tags (e.g., Arc163).

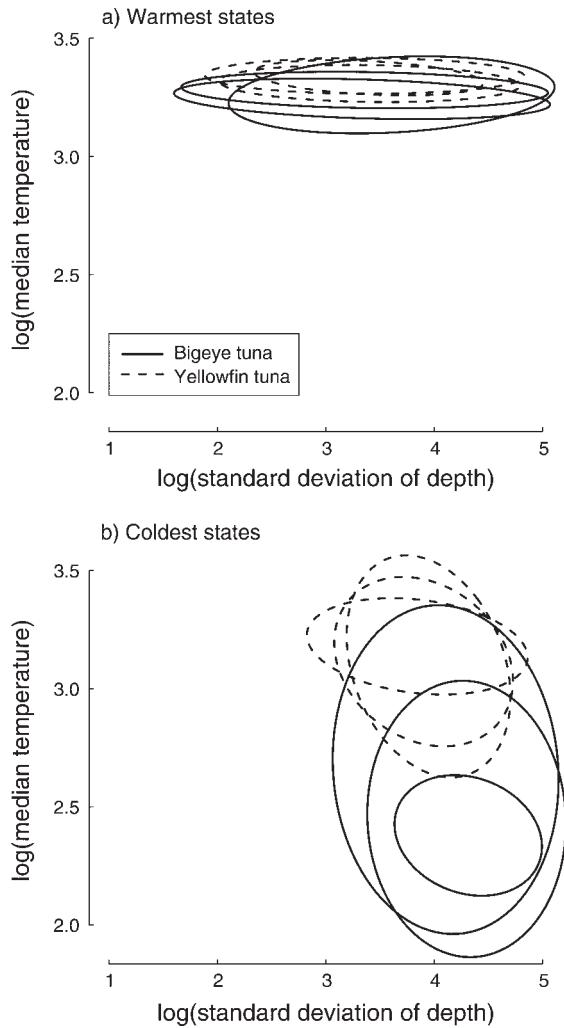


FIG. 4. Results from the hidden Markov models (HMMs) estimated on archival tag time series for two tuna species, showing plots of multivariate-normal behavioral-state distributions. Each individual fish has (a) a warm and (b) a colder state, described in multivariate space. Ellipses represent the mean and variation of state distributions to a 95% confidence interval for each state.

In this application, a covariate representing diel period has been included as part of a linear equation defining the transition probabilities. A concise way to summarize the information in the Markov transition matrix is to calculate its equilibrium state, also called the stationary distribution. In the case of behavioral time series, the stationary distribution can be thought of as the proportion of time an individual would spend in each state if the time series continued indefinitely. Thus, a transition matrix can be viewed as a vector, where each value is the proportion of time at the limit spent in each motivational state. Here, we use stationary distributions to examine estimated transition matrices.

Fig. 5 shows the two stationary distributions for all fish, one each for day and night. There are clear differences in behavioral switching from day to night in all individuals. All fish, except the yellowfin individual Arc269, have a large probability of switching to their respective cold states during the day. In

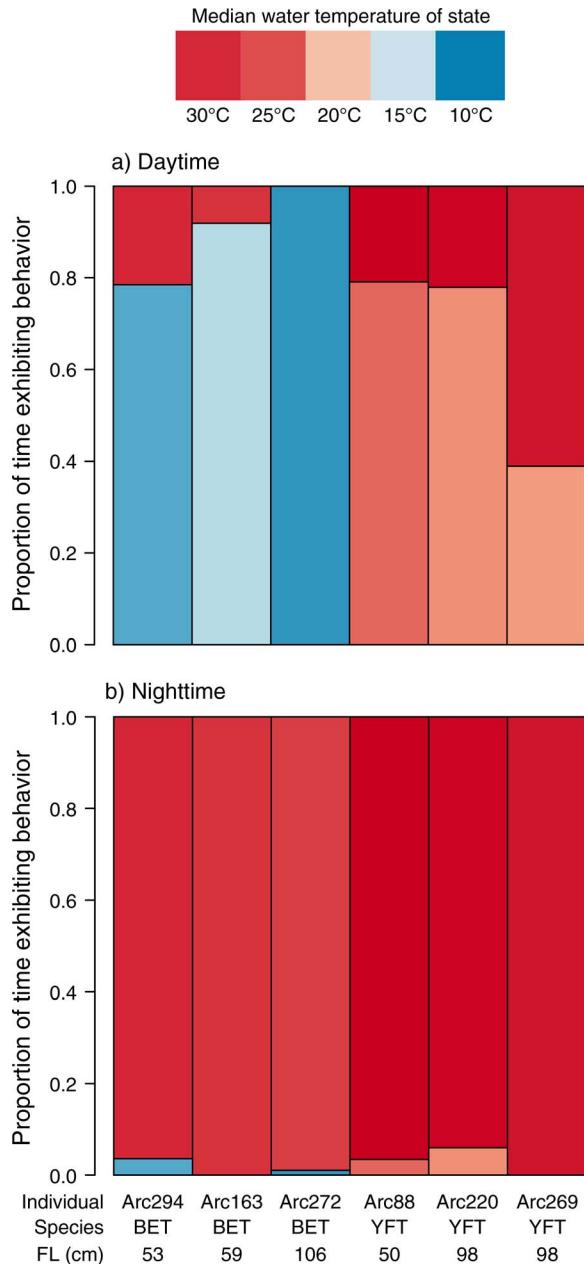


FIG. 5. Estimated transition matrix stationary distributions during (a) daytime and (b) nighttime hours for individual bigeye tuna (BET) and yellowfin tuna (YFT). Bars represent proportions of time exhibiting behavioral states in the limit for each fish, with colors indicating the back-transformed distribution mean of that state, in the temperature dimension. Fork length (FL) is the straight-line measurement from the tip of the snout to the edge of the central caudal fin rays.

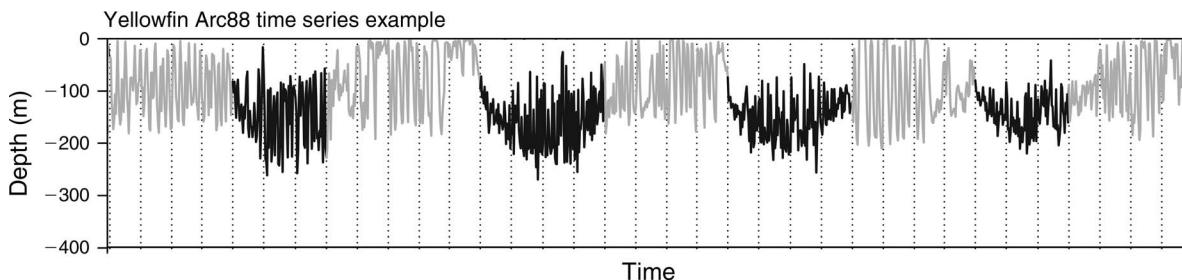


FIG. 6. Example section of raw dive data from a small yellowfin tuna, Arc88, automatically classified into either warm-state (gray) or cool-state (black) sections of three hours using a two-state HMM; vertical dotted lines demarcate the subsection boundaries.

contrast, all individuals exhibit an even greater probability of switching to their warm state during the night, with a very small chance of switching back to colder states. In the cases of the bigeye tuna Arc272 during the day and Arc163 during the night, the probability of switching away from these persistent states is actually zero.

Time series were classified by computing the most likely sequence of states from the given observations using a backward-smoothing filter on the state probabilities (Wikle and Berliner 2007). Each state is given a probability of occurrence for each observation in the time series, and the largest probability was chosen as the classification of behavior at each time step. An example of how these automatic classifications relate to the raw dive data is shown in Fig. 6. The effect of day and night is clearly seen in the classification, although 3-h sections of warm state behavior occasionally still occur during the day. Note that the variation in amplitude is much greater for warm-state behaviors, exhibiting both tight association at a particular depth and large movements through the water column during a 3-h period. In contrast, the classified cold states are always associated with larger movement through a range of depths.

#### DISCUSSION

Results from the simulation experiments demonstrate the effectiveness of our approach in describing and identifying underlying states from multivariate mixed distributions. When states are well separated and persistent, identifying a “knee-bend” in the log-likelihood across increasingly complex models appears to be a clear, although not fully objective, method for selection of the most appropriate model. However, as in the case of the more complex second scenario in which states are more diffuse in both distribution and persistence, changes in log-likelihood from one state to the next may be more gradual. Given the problems of using AIC and automatic model selection in HMMs, careful consideration and examination of both the estimated state distributions and pseudo-residuals should be undertaken for log-likelihood curves that do not exhibit a sharp bend. Alternative Bayesian methods

such as Markov chain Monte Carlo (MCMC) could also be employed to estimate posterior probability distributions, and potentially utilize Bayesian  $P$  values for assessing goodness of fit (Holan et al. 2009). MCMC sampling can be more computationally intensive, but if the numerical likelihood estimation approach that we suggest here does not provide clear indications for model selection, then these alternative methods should be considered.

Despite the complexity of the second simulated scenario, which contained significant overlap in distributions and transition parameters incorporating covariate information, the mean correct classification success rate was still over 90%. State distributions were accurately estimated, with consistently low error for multivariate means in particular. However, states estimated with large variance–covariance and low-persistence transition probabilities should be interpreted with particular caution.

In the application for tropical tuna species, our aim was to examine the way in which real-world continuous dive data can be described and classified using multivariate-normal HMMs, and to determine if the results were consistent with known ecology. Consideration of our 3-h temporal scale is critical when comparing our results to previous studies. At this scale, we do not identify fine-grained changes in movement (e.g., Sims et al. 2008, Humphries et al. 2010), individual dives (e.g., Dagorn et al. 2006), or longer-term composite dive profiles (e.g., Schaefer et al. 2007, Wilson and Block 2009). Rather, we aim to describe behaviors that occur at the scale of feeding and fishing events. Furthermore, it is important to stress the potential effects of our sectioning method. The value of the diel state covariate is based on the estimated day and night points from the split-moving-window analysis during pre-processing. This approach inherently estimates points of marked change in vertical movement, and so the strong effect of the diel covariate in state-switching within the model is not surprising. However, the HMM allows us to quantify this assumed relationship with transition probabilities. A full analysis should explore a more appropriate sectioning method using either depth-



PLATE 1. Yellowfin tuna being thrown back into the sea immediately post-tagging. Photo credit: J. Scutt Phillips.

corrected light data, if available, or a behavioral-based method that allows drift in dawn and dusk due to seasonal changes or migration.

In this small sample of tropical tuna, all individuals exhibited behavioral states centered in warm surface waters that are very similar to one another. It is characterized by low changes in temperature but considerable variation in movement through the water column. The thermal biology of tropical tuna requires them to reside predominantly in warm waters. Given that the warm surface layer of the tropical Pacific is well mixed, it is unsurprising that the variation in temperatures is small and similar for all individuals in this warm state. These states were centered between 3-h medians of 25.6°C and 28.2°C, comparable to mixed-layer behaviors elsewhere described as surface-associated or type I behavior (e.g., Schaefer et al. 2007, Schaefer and Fuller 2010). The variation in standard deviation of depth was large, suggesting that these behaviors are neither highly depth-associated nor transient; rather, individuals exhibit a continuous range of variation in the depths that they occupy for this state.

The behavioral states centered in colder water are more varied across species. In all cases, individuals have a looser association with a particular depth in their cold states than in the warm states. This is consistent with observations that tropical tuna are required to return to warmer layers of water for thermoregulation (Holland et al. 1992) and possibly to repay oxygen debt (Prince and Goodyear 2006). Tropical tuna have evolved different ways to dive and exploit prey in colder layers of water (Dagorn 2000, Musyl et al. 2003), and it appears that this is reflected in how the two species examined here exhibit

deeper behavior. The cold states of all three yellowfin tuna were considerably warmer than those of the bigeye, with the two larger fish having almost identical distributions. The three bigeye also had colder states that were similar to each other, although distributions were centered between 10.8°C and 14.3°C, demonstrating a greater range of median temperatures than for the yellowfin.

The stationary distributions of the transition matrices show very clear differences in behavior between day and night. The known foraging ecology of tropical tuna suggests a preference for following diurnally migrating prey species for those individuals that are physiologically capable (Bertrand et al. 2002, Graham et al. 2006), and our results in this regard clearly align with the observations of many previous studies. For the majority of individuals, a strong tendency to switch to warm states during the night and colder states during the day was exhibited. The persistence for warm states during the night was demonstrated by an almost zero chance for all fish of switching from these behaviors during this time. In contrast, behavioral states during the day were more varied, particularly for the yellowfin examined here, with only the largest bigeye tuna displaying a complete lack of switching from deep cold states during the day. Such “uncharacteristic” daytime switches to shallow warm behavior have previously been ascribed to association with floating objects (Schaefer and Fuller 2010), and these results potentially reflect the same behavior.

In this study we have demonstrated a technique for objectively characterizing continuous ecological data, summarizing time series at a temporal scale of interest into a multivariate assemblage. Dimensions are chosen

that both represent the variation in qualitative patterns observed in previous studies and relate to drivers of the phenomenon we wish to investigate, allowing straightforward incorporation into a HMM. Classification of the time series is objective and probabilistic, and provides a simple and easily interpretable way to examine if patterns are observed across factors that can then be reincorporated as parameters within the transition matrices or state distributions themselves of an updated HMM. Data from any number of sources can be arranged into a general,  $k$ -dimensional, and multivariate distribution as the observation model, and any combination of other distributions more appropriate to the data can be used (Peel and McLachlan 2000). In addition, information that does not form the behavioral observation model of the animal, but is believed to influence either the switching between these behaviors, the nature of the behaviors themselves, or both, can be included as covariate parameters. Although increasing the amount of data used in estimation of the likelihood will improve model fitting, the parameter space of a multivariate HMM will increase nonlinearly due to the increasing size of the transition and variance-covariance matrices, so care must be taken when fitting overly complex models. Furthermore, the simulation experiments described here have demonstrated where we might have the most confidence in estimated parameters of a HMM, i.e., the means of multivariate state distributions and the parameters of nontransitory states.

Information on the movement behaviors of marine animals exists for many species across a wide range of environments and bio-logging experiments (Block et al. 2011), and a broad range of methods have been applied to classifying and interpreting these data (e.g., Schaefer et al. 2007, Sims et al. 2009, Chiang et al. 2011). The strength of the analytical approach we have taken here is twofold. First, we do not simply assume the influence of explanatory variables on an abstract description of an animal's behavioral space such as a depth frequency distribution. Rather, as with previous studies using HMMs for ecological data, behavioral states are objectively estimated and based on dimensions that have been chosen to provide model outputs that may have direct interpretations. Second, this approach is applicable to many different types of ecological data taken from uncertain and imperfect observations. Frequency and location of acoustic-tag movements between receivers could be arranged as multivariate time series to classify habitat use of animals in river systems (e.g., McMichael et al. 2010), whereas periodic immersion data combined with GPS tracks from bio-logging equipment on birds can be used to examine at-sea foraging behaviors (e.g., Guilford et al. 2009). Here we have used an example from data on the vertical behavioral classification for tropical tunas in the Western and Central Pacific

Ocean, which forms a key component in quantifying the vulnerability of fish to surface gears in an industry generating at least US\$3000 million per year. However, HMM analyses of summary metrics taken from multivariate time series provide easily interpretable models for the objective classification of many different types of autocorrelated ecological data. Both the nature of, and switching between, states can be examined, and HMMs representing alternative hypotheses on the mechanisms driving these patterns can be compared to better understand changes in ecologically relevant states.

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## SUPPLEMENTAL MATERIAL

## Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-0862.1.sm>